

A EUTHYCARCINOID ARTHROPOD FROM THE SILURIAN OF WESTERN AUSTRALIA

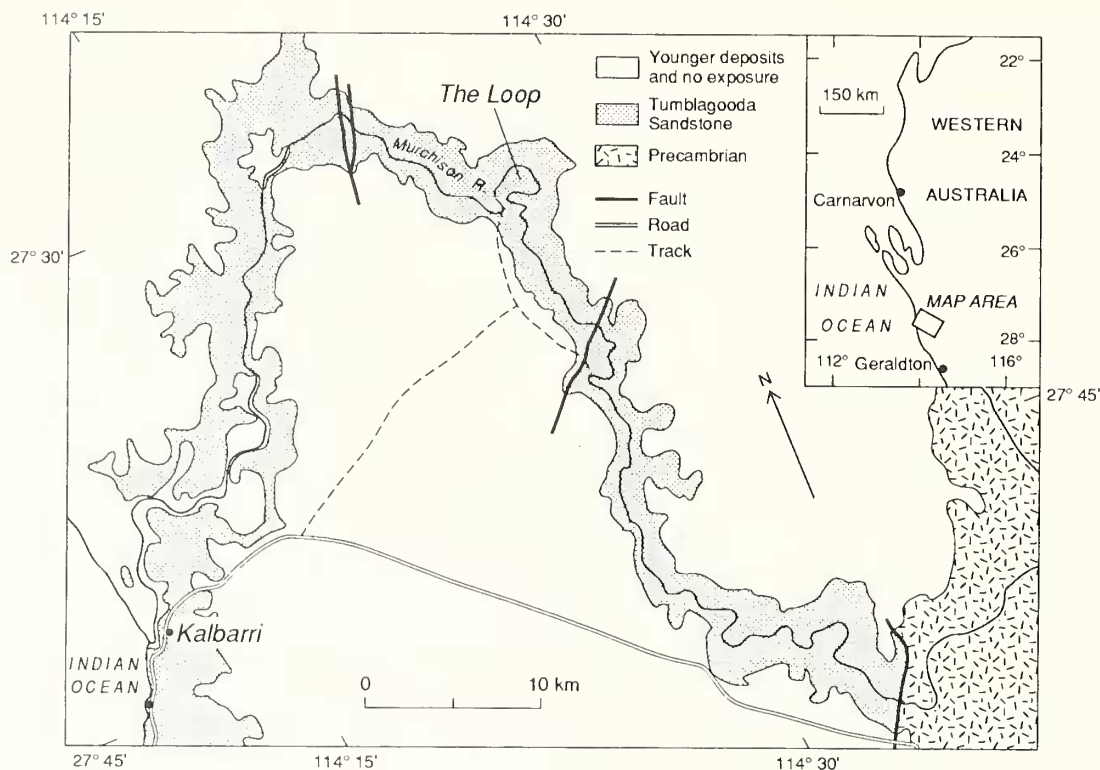
by KENNETH J. McNAMARA *and* NIGEL H. TREWIN

ABSTRACT. The Euthycarinoidea is a superclass of the arthropod phylum Uniramia and one of the rarest groups of fossil arthropods. Only seven species in five genera have been described, from rocks of Late Carboniferous age in France and the USA, and of Middle Triassic age in France and eastern Australia. Here, a much older euthycarcinoid, from a mixed sequence of fluvial and aeolian sandstones of probable Late Silurian age in Western Australia, is described as *Kalbarria brimmellae* gen. et sp. nov. Because of their uniramian affinities, it has previously been suggested that euthycarcinoids may be the closest ancestral relatives of hexapods. Although previous evidence had indicated that the earliest hexapod predated the earliest euthycarcinoid, the discovery of a euthycarcinoid about 120 million years older than the previous oldest record, and predating the oldest known hexapod, provides strong support for the view that the hexapods may have evolved from the Euthycarinoidea. A model illustrating euthycarcinoid origins from myriapods, and hexapod origins from euthycarcinoids is proposed, based on paedomorphic loss of appendages.

IN July 1990 a single specimen of a fossil arthropod (Western Australian Museum specimen number WAM 90.158) was collected from the rim of the Murchison River gorge in Western Australia (Text-fig. 1). The fossil (Text-fig. 2) came from the Tumblagooda Sandstone, a unit that exceeds 1000 m in thickness in the Murchison section. The part of the sandstone sequence from which the fossil was collected was interpreted by Hocking (1981, 1991) as having been deposited in a mixed braided fluvial and aeolian sandsheet environment. However, Trewin (1993) reinterpreted it as a mixed fluvial and aeolian sandsheet deposit. The arthropod is the first body fossil to be collected from the Tumblagooda Sandstone, despite the presence of a rich trace fossil assemblage (Trewin and McNamara work in progress), in particular extensive trackways thought to have been made by a number of different types of arthropods, including eurypterids (McNamara 1981).

AGE OF THE TUMBLAGOODA SANDSTONE

Although palaeomagnetic data have suggested an Early Ordovician age for the Tumblagooda Sandstone (Schmidt and Hamilton 1990), palaeontological evidence indicates that the sandstone is probably younger. Simple trilete spores and acritarchs recovered from borehole material attributable to the Tumblagooda Sandstone are indicative of a Silurian age (B. E. Balme, pers. comm.). Similarly, the Dirk Hartog Formation, which conformably overlies the Tumblagooda Sandstone, has yielded a conodont assemblage that indicates a Late Silurian age (Philip 1969). Most of the conodonts that were identified are long-ranging Ludlow species that extend into the Early Devonian. The presence of *Ozarkodina ziegleri tenuiramea* Walliser, 1964 and *O. aff. fundamentata* (Walliser, 1957) suggest a correlation with the mid-Ludlow *ploekensis* Zone. Higher in the unit the presence of *O. jaegeri* Walliser, 1964 and *Neoprioniodus bicurvatus* (Branson and Mehl, 1933) indicate a Late Ludlow age. The brachiopod *Conchidium* that was recovered from the Dirk Hartog Formation by Glenister and Glenister (1957) also suggests a Silurian age. It should be noted that the borehole from which this material was recovered is some distance from Kalbarri, making lateral facies variation a possibility and the correlation perhaps tenuous.



TEXT-FIG. 1. Locality map for the Murchison Gorge area of Western Australia, showing the extent of the exposures of the Tumblagooda Sandstone. The specimen described below was collected at The Loop.

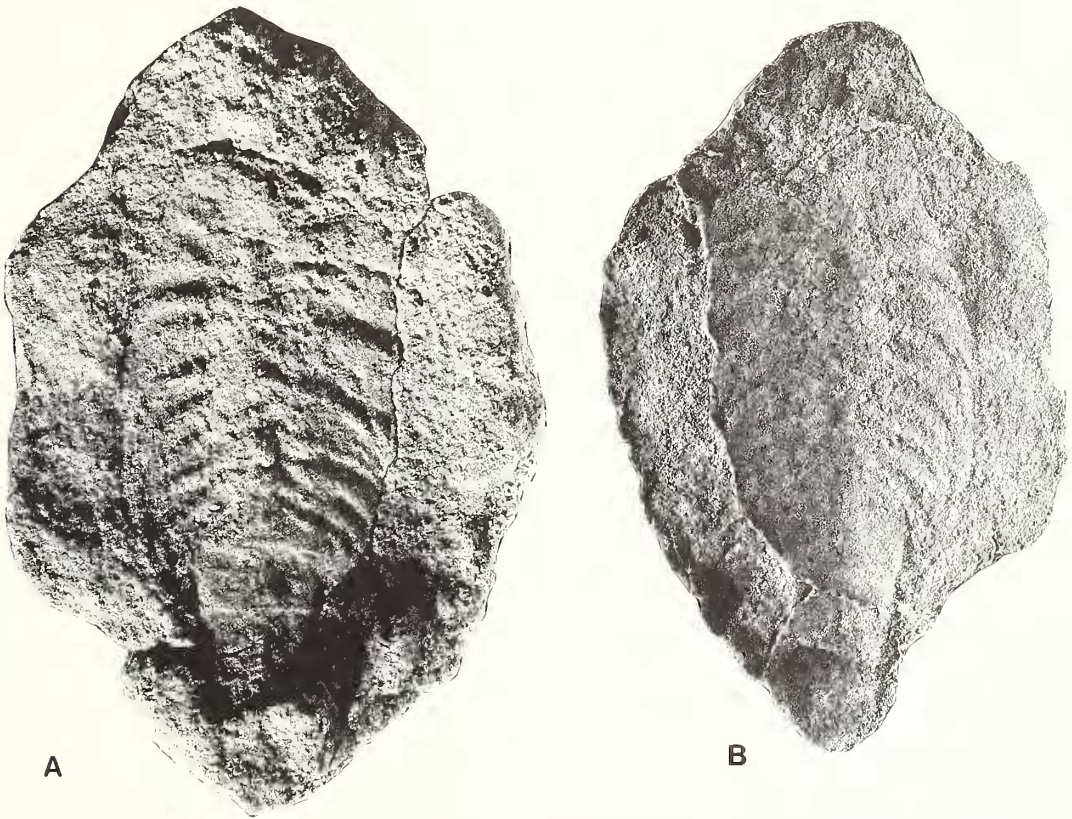
The trace fossil assemblage (Trewin and McNamara work in progress) is in many respects similar to a trace fossil assemblage in the Beacon Supergroup in Victoria Land, Antarctica (Bradshaw 1981; Gevers and Twomey 1982). In particular there are similar large trackways attributable to the ichnogenus *Diplichnites* (= *Beaconichnus*). Other ichnogenera in common include *Didymaulichnus*, *Beaconites*, *Diplocraterion* and *Heimdallia*. The lowest part of the Beacon Supergroup is dominated by a *Heimdallia*-*Diplichnites* ichnocoenosis (Bradshaw 1981). This ichnocoenosis is also a common component of the Tumblagooda Sandstone. While Bradshaw attributed a Devonian age to the lower part of the Beacon Supergroup, Gevers and Twomey (1982) noted that the upper part of the Beacon Supergroup contains Early to Middle Devonian lycopod stems (Plumstead 1964), suggesting that the lower part of the supergroup may extend possibly as low as the Silurian. Either way, the palaeontological evidence indicates a similar age for the two sequences, perhaps close to the Silurian-Devonian boundary.

Further argument against an Ordovician age is provided by the age of mineralization adjoining dolerite dykes in the Northampton Block, that occur immediately south of the exposure of the Tumblagooda Sandstone. This has been dated at 434 ± 15 Ma (i.e. Early Silurian), yet there is no evidence of this phase of mineralization having effected the Tumblagooda Sandstone (Blockley *in* Hocking *et al.* 1987).

PRESERVATION OF THE SPECIMEN

The fossil arthropod, which has a preserved length of 115 mm, occurs in a light brown, medium to coarse, quartz sandstone. The grains are between 0.1 and 1.0 mm in diameter, with most between 0.3 and 0.5 mm. The individual grains are well rounded and subspherical. The organism is preserved

as an external mould of the ventral surface, apart from the anteriormost tergite (T1) – the gnathocephalon, and presumed procephalon. Both of these elements were folded beneath the body prior to fossilization and are consequently preserved as external moulds of the dorsal surface, impressed on the ventral surface (Text-fig. 2A). By ‘unfolding’ the carapace, the original length of the arthropod would have been 133 mm. Subsequent attempts to locate the counterpart of the specimen, which presumably would have preserved the dorsal surface, proved unsuccessful, as were attempts to locate more specimens.



TEXT-FIG. 2. *Kalbarria brimmellae* sp. nov. Western Australian Museum specimen number WAM 90.158; holotype; Murchison River, Western Australia; (?) Late Silurian, Tumblagooda Sandstone, $\times 0.75$. A, external mould of the ventral surface in sandstone. B, latex cast.

Preservation of the arthropod in such a coarse-grained rock is surprising; not only are the tergites preserved, but so too are the appendages, implying that these elements were relatively well sclerotized. The ventral somites, however, are poorly preserved, suggesting that they may have been less well sclerotized.

The presence in the specimen of a small procephalon, six dorsal tergites and eleven preabdominal appendages, combined with an appendage-free abdomen of five segments, confirms the identification of the Tumblagooda Sandstone arthropod as a member of the Euthycarinoidea. This group of rare, exclusively freshwater arthropods has previously been known only from Late Carboniferous and Middle Triassic strata in eastern France, the United States and eastern Australia (Gall and

Grauvogel 1964; Riek 1964, 1968; Schram 1971; Schram and Rolfe 1982; Rolfe 1985). Euthycarcinoids are characterized by the possession of mono-, diplo- and/or triplopodous dorsal segmentation. The presence of a euthycarcinoid in the Tumblagooda Sandstone therefore extends the range of this superclass by about 120 million years, back into the Silurian.

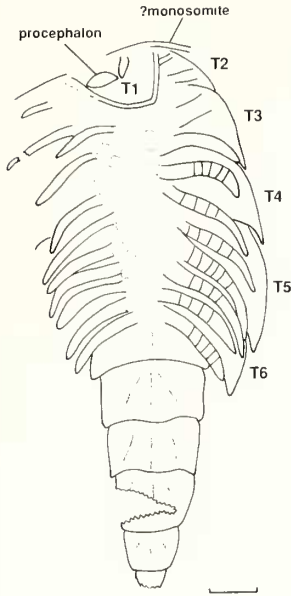
EUTHYCARCINOID RELATIONSHIPS

Until quite recently, this group of arthropods had proved hard to assign with confidence to any higher taxonomic group. Handlirsch (1914) indicated his belief that they were crustaceans in his choice of the name 'Euthycarcinoidea' (literally meaning 'straight crab'), when describing the first known species, *Euthycarcinus kessleri*, from the Triassic of eastern France. He considered that euthycarcinoids represented a primitive form of copepod crustacean. When they redescribed *E. kessleri*, Gall and Grauvogel (1964) placed it in a separate new class of crustaceans. However, as Schram (1971) noted, euthycarcinoid segmentation bears little resemblance to that of any other known group of crustaceans. Furthermore, Schram (1971) observed that the 'mandibles' and postoral appendages are very obscure in euthycarcinoids and do not indicate the phylogenetic relationships of the group.

Schram (1971), in describing *Kottixerxes gloriosus* from the Late Carboniferous at Mazon Creek, USA, preferred to include the euthycarcinoids in the Merostomoidea, as a distinct order. Riek (1964) had earlier considered *Synaustrus brookvalensis*, the species that he described from the Middle Triassic of New South Wales, Australia, to be a merostomoid trilobitoid. However, following the publication of Gall and Grauvogel's (1964) paper, and a re-examination of the material, Riek (1968) agreed with them on the more likely crustacean affinity of euthycarcinoids. But rather than viewing them as copepods, Riek suggested that they belonged in the Branchiopoda.

It was not until Bergström (1980) re-evaluated the phylogenetic relationships of early arthropods, including the euthycarcinoids, and new material from the USA (Schram and Rolfe 1982) and France (Heyler 1981; Rolfe *et al.* 1982; Rolfe 1985) was examined, that a new and more radical reassessment of the likely phylogenetic relationship, and hence systematic position, of the Euthycarcinoidea was made. All previous taxonomic assignments had inferred that euthycarcinoids possessed biramous appendages. However, as Bergström (1980) observed from studying *Synaustrus brookvalensis* and *Kottixerxes gloriosus*, euthycarcinoids possessed uniramous appendages. This was later confirmed by the studies of Schram and Rolfe (1982) on *Kottixerxes*, *Sottixerxes* and *Smithixerxes*, and supported by this study of the Western Australian euthycarcinoid. The presence of two pairs of antennae, such as Riek (1964, 1968) reported in *Synaustrus*, has not been substantiated, either by the re-examination of his material by one of us (K.J.M.), or by the study of other euthycarcinoid species. Furthermore, the absence of uropods makes crustacean affinities unlikely. The presence of diplo- and triplosegments, combined with a uniramous limb, led Bergström (1980) to state that the Euthycarcinoidea 'seem to show important similarities only with the uniramous groups and probably represent a distinct uniramous group comparable in rank with the Myriapoda and Hexapoda'.

In their review of the Carboniferous euthycarcinoids from France and the USA, Schram and Rolfe (1982) formalized Bergström's concept and recognized the Euthycarcinoidea as a subphylum of the Uniramia. However, the concept of the Uniramia *sensu* Manton (1977) as a separate phylum comprising the Onychophora, Myriapoda and Hexapoda has come under much criticism (e.g. Kristensen 1975, 1981, 1991; Patterson 1978; Boudreaux 1979). The general consensus is that, while the Hexapoda and Myriapoda can be regarded as sister-groups, the Onychophora represents a separate phylum from the Uniramia. While Boudreaux (1979) regarded the Hexapoda and Myriapoda as classes, Kristensen (1991) considered them to be superclasses, rather than subphyla. Kristensen pointed out how the Hexapoda and Myriapoda have been combined as either the 'Atelocerata', 'Antennata' or 'Tracheata'. However, there are problems with using any of these names. For instance, it is debatable whether the evolution of a tracheal system occurred only once during the evolution of the myriapod/hexapod lineage. The other alternative is to follow Harvey



TEXT-FIG. 3. *Kalbarria brimmellae* sp. nov. Camera lucida drawing based on latex cast of original (Text-fig. 2B). T1 to T6 are dorsal tergites 1 to 6, the lateral extremities of which protrude beyond the ventral appendages. The limb-bearing section comprises the preabdomen; the narrower, appendage-free section the postabdomen. Scale bar = 10 mm.

and Yen (1989) who used the concept of the Uniramia as a phylum exclusive of the Onychophora. This is followed here, with the Uniramia being considered to comprise the Hexapoda, Myriapoda and Euthycarinoidea.

Starobogatov (1988) proposed a new classification of the euthycarinoidea, incorporating the Cambrian arthropod family Aglaspidae. This group had been considered by other authors to be either xiphosuran merostomes (Stormer 1955), or a separate class of merostomes (Bergström 1971), while Briggs *et al.* (1979) doubted whether they were merostomes at all. From their redescription of *Aglaspis spinifer*, Briggs *et al.* (1979) deduced that the assignment of the aglaspids to the Merostomoidea was unwarranted. Although Repina and Okuneva (1969) had described what they interpreted as gill branches in the aglaspid *Khankaspis bzalnovi*, Briggs *et al.* (1979) considered that aglaspids had uniramous appendages. However, in their opinion more work needed to be done on elucidating the nature of aglaspid appendages before assignment to any class could be considered.

Starobogatov (1988), without further analysis of other material, accepted the uniramous nature of the limbs of aglaspids and placed them in the Euthycarinoidea. However, there are a number of major problems with this interpretation. Aglaspids, unlike euthycarinoidea, have a large headshield that incorporates at least four appendages (Briggs *et al.* 1979); a comparable headshield is not present in euthycarinoidea (Schram and Rolfe 1982). The thoracic segments are monosegments in aglaspids, unlike all euthycarinoidea where at least some of the segments are diplo- or triplosegments. Furthermore, there is no distinct postabdomen of five or six segments, such as occurs in euthycarinoidea. On these grounds alone there seems little justification for incorporating the aglaspids in the Euthycarinoidea. Hence in this paper the composition of the Euthycarinoidea is deemed to be the same as that envisaged by Schram and Rolfe (1982), with the addition of *Kalbarria*.

TERMINOLOGY

Schram and Rolfe (1982) considered that the small structure Bergström (1980) interpreted as the head was probably a procephalon, because in well-preserved material from elsewhere it was seen to carry a single pair of antennae, 'eyes' and the labrum. Previously, the first tergite had been interpreted as the head (e.g. Gall and Grauvogel 1964; Riek 1964). In their discussion of the uniramous affinities of euthycarinoidea, Schram and Emerson (1991) interpreted the structure,

referred to as 'tergite 1' by Schram and Rolfe (1982) and considered by them to be part of the preabdomen, as the gnathocephalon. There is some justification for this, in as much as the labrum (sternite 1 *sensu* Schram and Rolfe 1982, text-fig. 1) and sternite 2, thought to be involved with feeding, are situated beneath tergite 1. The small monosomite recognized in *Kottixerxes* and in *Sottixerxes* (Schram and Rolfe 1982) has been regarded as separating the preabdomen into two regions. Re-examination of the holotype of *Synaustus brookvalensis* by one of us (K.J.M.) has revealed that a similar small monosomite is present between tergites 1 and 2. Thus, in this study, tergite 1 is interpreted as the gnathocephalon, and tergites 2 and 6 part of the preabdomen, Schram and Rolfe (1982) referred to the small monosomite as tergite 1. However, as there was probably little dorsal expression of this somite it is not viewed herein as a tergite.

SYSTEMATIC PALAEOLOGY

Phylum UNIRAMIA Manton, 1973

Superclass EUTHYCARCINOIDEA Gall and Grauvogel, 1964

Family EUTHYCARCINOIDAE Handlirsch, 1914

Genus KALBARRIA gen. nov.

Derivation of name. After Kalbarri, Western Australia, the closest town to the site of discovery.

Type species. *Kalbarria brimmellae* sp. nov.

Diagnosis. Preabdomen broad, with five tergites of varying widths; tergite 1 less than half the width of tergite 5. Postabdomen relatively wide anteriorly, tapering strongly posteriorly. Postabdominal segments bearing ventral sagittal and diagonal ridges.

Kalbarria brimmellae sp. nov.

Text-figs 2-3.

Derivation of name. Named after Kris Brimmell who so astutely recognized the specimen in the field.

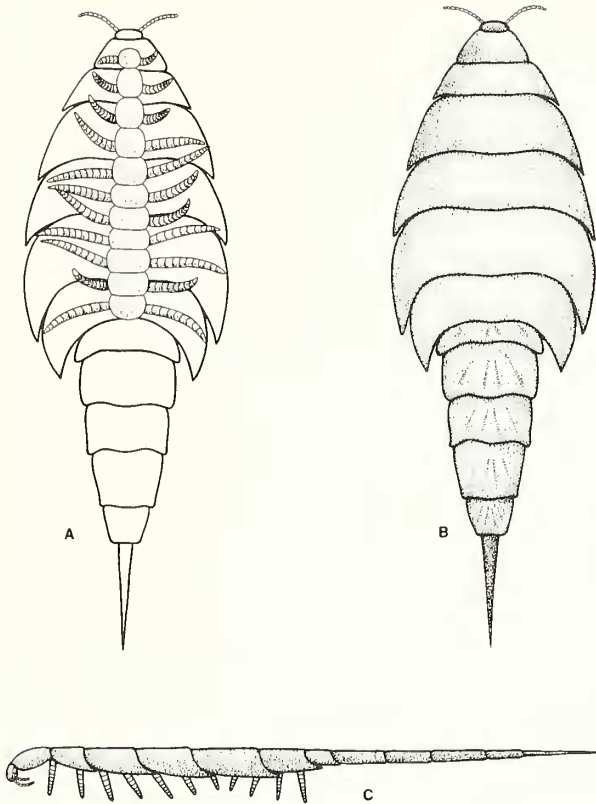
Holotype. Western Australian Museum specimen number WAM 90.158.

Locality and horizon. On the rim of the gorge of the Murchison River in the region of The Loop, near Kalbarri, Western Australia (Text-fig. 1); Tumblagooda Sandstone (? Late Silurian). Full locality details are kept on file in the Department of Earth and Planetary Sciences, Western Australian Museum, Perth.

Diagnosis. As for genus.

Description. Procephalon small, broadly ovoid, with a width (5.4 mm) twice that of its length; gently convex. Gnathocephalon (tergite 1) trapezoidal, with an anterior width the same as that of the procephalon, which is just 11.5 per cent of maximum preabdominal width (MPW); increases markedly in width posteriorly to 37 per cent MPW; occupies 17 per cent of combined gnathocephalic and preabdominal lengths; tergal margins gently curved. Thin, ridged structure situated between tergite 1 and tergite 2 may possibly represent the small monosomite observed in this position in *Kottixerxes gerem* (Schram and Rolfe, 1982, pl. 2, fig. 4).

Preabdomen progressively widens posteriorly from tergite 1 to tergite 5, then narrows to tergite 6. Relatively wide, length:width ratio of 1.54. Tergite 2 is a monosegment, reaching up to 88 per cent of MPW posteriorly; tergal margins very slightly curved and, like all subsequent tergites, subtended into slight postero-lateral prolongations. Tergite 3 is a diplosegment, reaching up to 96 per cent of MPW posteriorly, with slightly more curved tergal margins than the preceding two tergites. Tergite 4 is also a diplosegment and is slightly wider than tergite 3, attaining about 98 per cent of MPW. Tergite 5 is the widest and is a triplosegment; its tergal margin



TEXT-FIG. 4. *Kalbarria brimmellae*, sp. nov. Reconstruction of A, dorsal; B, ventral; and C, lateral views. Length of antennae and telson conjectural, as is size and shape of sternites, $\times 0.5$.

is slightly less curved than the preceding two tergites. Tergite 6, a diplosegment, is much narrower than the preceding segments, being only 70 per cent of MPW. Its postero-lateral margins are produced into quite prominent prolongations. Tergites show a progressive increase in length posteriorly, from tergite 2, which is 13 per cent of maximum preabdominal length (MPL), through tergite 3, 16 per cent of MPL, tergite 4, 18.5 per cent of MPL to tergite 5, 22 per cent of MPL. Tergite 6, as well as being narrower, is also shorter than preceding tergites, being 16 per cent of MPL.

Preabdomen with eleven pairs of uniramous appendages that do not extend laterally beyond the tergites. Compared with other described euthycarcinoid appendages, they are relatively stout. They have suffered slight post-mortem disarrangement, but show that they extend from the somites with a slight curvature. At about three-quarters of the transverse distance, they curve strongly backwards through an angle of between 50° and 60° . Proximally, the appendages are of similar diameter throughout (ranging between 3.0 and 3.4 mm) apart from the posteriormost which is slightly narrower at a diameter of 2.4 mm. Total number of segments in appendages not known, but in some appendages up to six segments are preserved, and these are wider than long. Appendages terminate in a single terminal spine.

The sternites, the ventral plate to which the limbs would have attached, are poorly preserved, due to their probably weaker degree of sclerotization.

Postabdomen of five gently curved segments; less than half width of preabdomen and two-thirds its length. Anterior segment chevron-shaped; width posteriorly 48 per cent of MPW; tapers strongly anteriorly to a width of just 20 per cent of MPW. Second segment rectangular, 47 per cent of MPW; wider than long, width being almost twice the length. Distal margins gently curved. Third segment widest anteriorly, being 41 per cent of MPW; tapers evenly posteriorly to 37 per cent of MPW; length similar to that of first segment, thus width is less than twice length, being 1.65 times length anteriorly, and 1.5 times length posteriorly. Fourth segment continues tapering trend, being only 25 per cent of MPW posteriorly; anteriorly width 1.47 times length, posteriorly 1.07 times length. Fifth segment tapers to just 21 per cent of MPW; anteriorly width 1.32 times length, posteriorly 1.19 times length. The anterior part of a sixth segment is just visible. This may represent the

proximal part of a telson. Postabdominal segments bear ornamentation of raised ridges that extend posteriorly and posterolaterally from the anterior margins of the segments.

Discussion. The fusion of the tergites is manifested in this specimen by the tergite 2 being a monosomite, tergites 3 and 4 being diplosegments, as is tergite 6, but with tergite 5 being a triplosegment. This sequence differs from all other known euthycarcinoids. However, Schram and Rolfe (1982) did not place great reliance on this character as a differentiating feature, considering that the diplo- and triplotergites were able to move relative to the sternites, as they were connected by arthrodial membranes.

The small, oval structure impressed on the folded-under tergite 1 is interpreted as the procephalon, in part because this ovoid shape would appear to be characteristic of euthycarcinoid procephala, as interpreted by Schram and Rolfe (1982, Text-fig. 1), but also because its longer dimension is similar to the anterior width of tergite 1, to which the procephalon would have been attached. Due to its relatively poor state of preservation, it is not possible to determine the nature of the eyes of *Kalbarria*. Preservation of the procephalon and tergite 1, the gnathocephalon, impressed beneath tergite 2 and part of tergite 3, is not surprising. Schram and Rolfe (1982) suggested that the procephalon in euthycarcinoids may have been carried in a vertical orientation, much as in some insects and myriapods. The inverted preservation of the cephalon, plus tergite 1 suggests the possibility that during life tergite 1 may also have been orientated at a higher angle to the horizontal plane, than other tergites (Text-fig. 4). The location of the small monosomite between the preabdomen and gnathocephalon is likely to have been a site of greater articulation.

In reconstructions of other euthycarcinoids (e.g. Schram and Rolfe 1982, text-fig. 2) where appendages are depicted, they are shown as projecting laterally beyond the tergites. This would not appear to have been the case in *Kalbarria*, the ventral aspect of the preservation revealing that the gently curving appendages do not project beyond the distal margins of the tergites. The relatively consistent degree of limb curvature suggests that it had limited ability to flex. While the total number of segments in each appendage is not known, the sizes of those that can be identified indicate that it was unlikely that there were as many as the twenty-four reported in *Kottixerxes gloriosus* (Schram and Rolfe 1982, p. 1437). The size of the leg segments of *Kalbarria* suggest that there were less than half this number present.

A number of previously-described euthycarcinoids are characterized by the possession of well-developed setae on their appendages, one per segment. In the case of *Kottixerxes gloriosus* they are developed as long, flap-like structures (Schram and Rolfe 1982, pl. 1, fig. 3). Although the appendages in *Kalbarria brimmellae* are not as well preserved as in *Kottixerxes gloriosus*, there is no evidence of the possession of setae. The impression made by the appendages in *Kalbarria brimmellae* indicate a moderately convex, cylindrical appendage. Compared with other euthycarcinoids the appendages are appreciably wider. It is therefore possible that a primitive character in euthycarcinoids was the possession of a walking leg that was shorter and stouter than in later euthycarcinoids and was either free of setae, or at the most possessed only very fine setae.

Apart from its relatively greater width, the postabdomen differs little in overall structure from other euthycarcinoids. It does, however, bear ornamentation not recorded in other species, in the form of both sagittal and oblique ridges on the ventral surface. Whether or not these were also present on the dorsal surface and on the preabdomen is not known.

Of other euthycarcinoids, *Kalbarria* most closely resembles species of the Late Carboniferous *Kottixerxes* and the Middle Triassic *Synaustus*. Like *Kalbarria*, both have a preabdomen composed of five tergites and an appreciably smaller postabdomen, a characteristic feature of the family Euthycarcinidae. *Kalbarria* can be distinguished from the two species of *Kottixerxes* (*K. gloriosus* from the Late Carboniferous at Mazon Creek, Illinois, USA and *K. gerem* Schram and Rolfe, 1982 from the Upper Carboniferous at Montceau-les-Mines, France) by virtue of its larger size, broader, more elliptical, preabdomen and broader, more strongly tapering postabdomen that bears an ornamentation of posteriorly diverging, straight ridges. It similarly differs from the Middle Triassic *Synaustus brookvalensis* (see Riek 1964, 1968) in its larger size and relatively broader preabdomen

and postabdomen. Although Riek (1964, 1968) considered that *Synaustus* possessed only four postabdominal segments, re-examination of the original material shows that, like other euthycarcinids, it too possessed five.

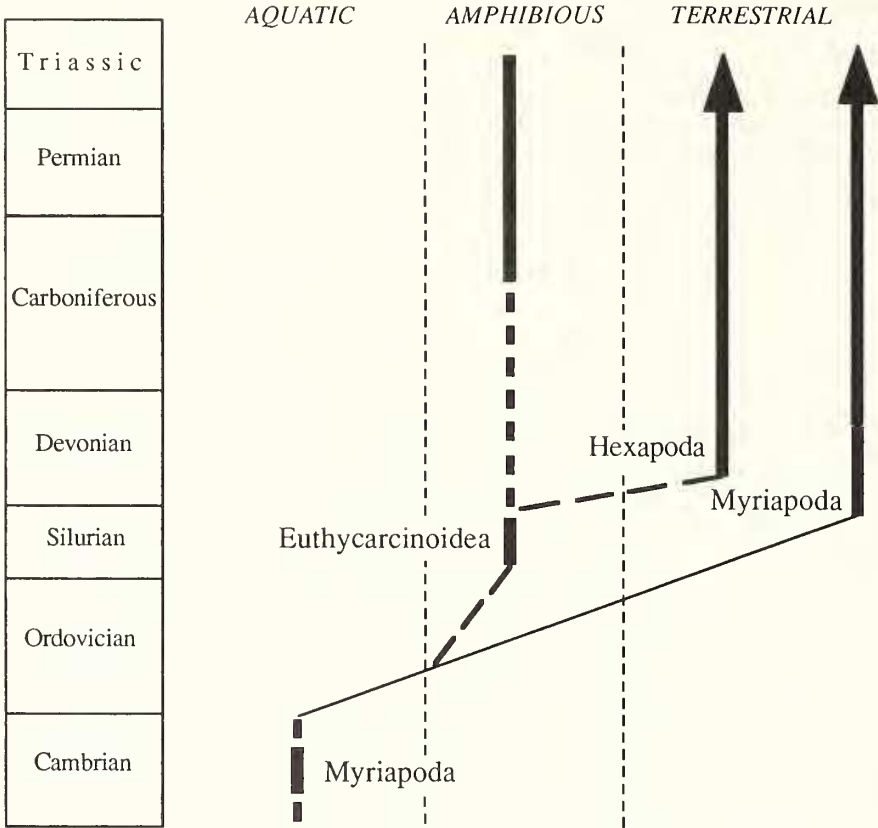
Kalbarria brimmellae bears a superficial resemblance to the Late Devonian *Oxyuropoda ligioides* Carpenter and Swain, 1908, an arthropod of uncertain status that has at various times been referred to the Tanaidacea, Isopoda, Arachnomorpha and the Phyllocarida (Rolfe 1969). However, unlike *K. brimmellae*, *O. ligioides* possesses a more parallel-sided body, very much shorter postabdomen, and paired caudal rami. Although nothing is known about the appendages of *Oxyuropoda*, the overall similarity to the euthycarcinoid bodyplan indicates that, as Schram (1971) suggested, further consideration should be given to including this form within the Euthycarcinoidea.

EUTHYCARCINOIDS AND THE EVOLUTION OF THE HEXAPODA

Heterochrony and the myriapod–euthycarcinoid–hexapod transition

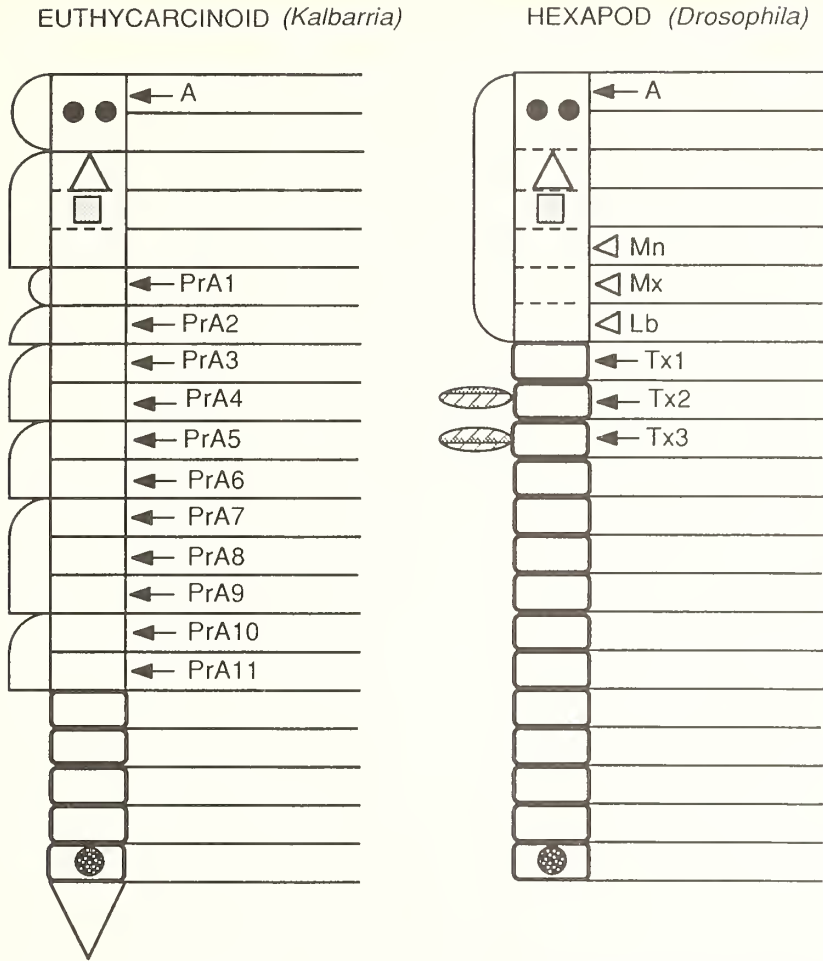
Perhaps the most radical suggestion made by Schram and Rolfe (1982, p. 1448) was that the Euthycarcinoidea may have been involved in the evolution of the Hexapoda: '...the dramatic reduction of limbs noted between [*Sottixerxes* and *Kottixerxes*] during... phylogeny, might be regarded as an interim stage en route to hexapody...'. The ancestors of hexapods, like most other major groups of organisms, are unknown. To many workers the most plausible explanation for the evolution of the Hexapoda has been that they derived from some hypothetical myriapodous ancestor (de Beer 1958; Anderson 1973; Manton 1977; Mamayev 1977; Manton and Anderson 1979; Boudreaux 1979; Little 1983; Anderson 1987; Kristensen 1991). Anderson (1987) postulated that a group of hypothetical myriapods might have hatched as hexapodous juveniles, then subsequently produced a further eleven leg-bearing segments through ontogeny, to reach sexual maturity with a complement of fourteen pairs of trunk limbs. By progenesis (paedogenesis of Anderson 1987) at a juvenile stage, when only three pairs of appendages had been produced, an adult organism would have existed that possessed just three pairs of appendages, such as in hexapods. While there is little doubt that heterochrony has played a major role in evolution in most, if not all, groups of organisms from the intraspecific to the suprageneric level (McKinney and McNamara 1991), such a scenario is little more than speculation. While it might be argued that the Euthycarcinoidea are too specialized a group to be the ancestors of another subphylum, such arguments are based purely on consideration of the morphological features of the adult organism. As it seems likely that the mechanism for the evolution of hexapods was paedomorphosis, operating at early stages of development of the ancestor, it would have been the morphologically much simpler juvenile form that would have been the target of selection. While little is known of early euthycarcinoid development, Schram (1971) described a juvenile of *Kottixerxes gloriosus* only 14 mm long. It had eleven preabdominal segments, but differed from adults in the absence of fusion of the tergites, indicating the more generalized form of juveniles.

The recognition that euthycarcinoids belong in the same phylum as the hexapods and myriapods, and are characterized by one major feature that is present in hexapods but lacking in myriapods, the subdivision of the postcephalic segments into limb-bearing and limb-free sections, makes them the most suitable candidate amongst known organisms for being ancestors of the hexapods (Text-fig. 5). Their multilimbed state and less complex head region are both more primitive states than corresponding structures in the hexapods. However, while their subdivision into a pre- and post-abdomen is a more derived state than in the myriapods, their cephalic region is more primitive than in living myriapods. Whereas myriapods have only limb-bearing postcephalic segments, in hexapods there are three pairs of limb-bearing postcephalic segments (the thorax) followed by eleven or fewer limb-free segments (the abdomen), making a total of 14 post-cephalic segments. In euthycarcinids there are eleven limb-bearing segments (the preabdomen), followed by five limb-free segments (the postabdomen). Schram and Rolfe (1982) considered that in *Kottixerxes gerem* there are eleven limb bearing segments plus one or two limb-free segments in the preabdomen. This would



TEXT-FIG. 5. Stratigraphical ranges of euthycarcinoids, hexapods and myriapods in the Palaeozoic, and their suggested relationships. Note the general trend to terrestriality through time.

seem to indicate that in euthycarcinids there are up to eighteen (Text-fig. 6) post-cephalic segments. The euthycarcinids would thus seem to be over-endowed with segments, as Anderson (1987) had considered that the hexapod ancestor would require a total of fourteen trunk segments. However, as Schram and Rolfe (1982) pointed out, the euthycarcinoid head would appear to be much simpler than the hexapod head, which is known to be composed of six basic segments, fused into a cephalon, plus an antennate segment (Text-fig. 6). While the cephalic region of euthycarcinoids is still poorly known, it would seem that it might correspond to a procephalon, consisting of a single pair of antennae and sphaeroidal 'eyes', plus a gnathocephalon. Schram and Emerson (1991) pointed out that 'The...head is not well known, but appears to resemble Snodgrass' (1952) hypothetical primitive arthropod head, with an anterior procephalon bearing a single pair of antennae and a distinct posterior gnathocephalon bearing the mouth and a set of rarely preserved mandibles.' Schram and Rolfe (1982) hypothesized that formation of the gnathocephalon might have occurred by fusion of the first three euthycarcinoid post-procephalic segments. To form the hexapod head, this gnathocephalon would have had to have fused to the procephalon and a further two segments (PrA1 and PrA2 of Text-fig. 6) would have been needed to be incorporated into the head region. If this were the case, with the preabdomen losing two limb-bearing segments to the conjoined procephalon and gnathocephalon, then fourteen post-cephalic segments would remain, the same as in the hexapods (Text-fig. 6), PrA3-PrA5 of the euthycarcinoid being homologous with the three



TEXT-FIG. 6. Schematic representation of the segmentation of a euthycarcinoid (*Kalbarria*) and a hexapod (*Drosophila*). Representation is based on Schram and Emerson (1991, figs 9–10), the euthycarcinoid being represented by *Kalbarria*, rather than *Kottixerxes*. One difference in the interpretation is that Schram and Emerson (1991) assumed that each postabdominal segment in the euthycarcinoid was a duplosomite. There is no evidence for this, and it is herein suggested that each segment equates to a monosomite. This interpretation results in the anus being on the 21st monosomite in both euthycarcinoids and hexapods. In this model the three hexapod thoracic segments are considered to be homologous to the euthycarcinoid preabdominal segments T3 to T5. Abbreviations: A, Antennate somite; PrA, Preabdominal somites; Mn, Mandibular somite; Mx, Maxillar somite; Lb, Labial somite; Tx, Thoracic somite. Symbols: small circles = eyes; triangle = labrum; square = mouth; shaded large circle = anus; black arrows = appendage-bearing somites.

appendage-bearing segments of the hexapod thorax (Tx1-Tx3 of Text-fig. 6). With this model, the anus would be on the homologous segment in the euthycarcinoids and hexapods, the terminal segment.

The second change that would have occurred in the transition from a euthycarcinoid to a hexapod would have been the suppression of development of the posterior six pairs of appendages by pedomorphosis. However, there would have been retention of the same number of segments, these becoming part of the post-abdomen (= abdomen in hexapods). Typically in uniramians, segmentation precedes formation of appendages, limb primordia being established shortly after the

blastoderm stage, at which time the embryo has been subdivided by the activity of segmentation genes (Cohen 1990). Detailed experimental work on *Drosophila* has shown how one specific gene, the *Distal-less* gene, plays a crucial role in controlling the position of limb formation. Its activity is exerted by differential regulation of subordinate genes. In experimentally induced mutants in which the *Distal-less* gene is deleted, the primordia of the appendages are not developed. As Cohen (1990) noted, because *Distal-less* gene acts as a developmental switch defining the identity of cells as limb, activation of expression of this gene is crucial in determining limb primordia in the embryo. If, as seems likely, such a gene system operated in euthycarcinoids, then it could be suggested that suppression of expression of this gene would have resulted in failure of some appendages to develop. It can be conjectured that during euthycarcinoid ontogeny the full complement of cephalic and post-cephalic segments was formed, following which pairs of appendages developed sequentially from the anterior to the posterior, as in other uniramians (Boudreaux 1979; Minelli and Bortoletto 1988; Cohen 1990).

While the number of appendages is fixed very early in embryological development in the hexapods, the full number in some myriapods is not attained until after a number of post-larval moults. For instance, in symphylan myriapods (Ravoux 1962) the newly hatched larvae possess five to seven pairs of legs (Boudreaux 1979). After three moults, the ninth segment develops a pair of legs (the preceding segments each having already developed a pair of legs earlier in development). After two more moults, legs have developed on the tenth and eleventh segments, but the twelfth and thirteenth segments are appendage-free. Precocious maturation in such forms could have the effect of producing an adult form with fewer appendages than its ancestral adult, but with retention of appendage-free posterior segments. Boudreaux (1979) noted how a number of 'specialised' millipedes fail to develop legs on the last few segments. This he attributed to 'neoteny' (= paedomorphosis).

With such a propensity in myriapods for paedomorphic loss of posterior limbs, it would not seem developmentally too difficult for an ancestral form to have ceased limb generation at an earlier ontogenetic stage, while segments were still generated at the ancestral rate. Such dissociated heterochrony is quite common in many groups of organisms (McKinney and McNamara 1991). The paedomorphic reduction in limb number could have occurred by one of three methods: (1) by premature maturation (progenesis), following production of only three pairs of appendages; (2) by a delay on timing of onset of appendage development (postdisplacement); or (3) by a reduction in the rate of appendage development resulting in cessation of production of further pairs of appendages. Either of the first two processes are the more likely. However, whichever paedomorphic process was involved, a form would be produced with three pairs of appendages, and a postabdominal, limb-free region of eleven segments, as is the case in the hexapods. Both of these seemingly major structural changes (the fusion of anterior dorsal segments, and the increase in number of postabdominal segments at the expense of the preabdomen) merely continue the trends apparent from a hypothetical evolution of euthycarcinoids themselves from myriapods (Text-fig. 5), and myriapods from a lobopod ancestor. Reductions in both segment and limb numbers could quite plausibly have been induced by perturbations to the gene regulatory system, principally by failure of specific genes to trigger segment or appendage formation in the later stages of early embryonic development.

One area where some of the later euthycarcinoids seem to differ appreciably from other uniramians is in the number of leg segments. *Kottixerxes* has up to twenty-four segments (Schram and Rolfe 1982). However, *Euthycarcinus* would appear to have had only twelve (Gall and Grauvogel 1964). From the size of those present in *Kalbarria*, a similar number to *Euthycarcinus* might be postulated. Kristensen (1991) considered that the relatively few number of leg segments (six) in hexapods is another hexapod autapomorphy. However, some have an extra four, which is the number present in Palaeozoic myriapods. The morphological significance of these numbers remains debatable. Kukalová-Peck (1987) considered that the hexapod leg evolved from an ancestral leg with a groundplan of no fewer than eleven segments. Again, the smaller number of leg segments in living hexapods argues for a paedomorphic reduction in number.

Like euthycarcinoids, myriapods possess diplosegments, but they have many more body segments (up to 191 in some Geophilomorpha – Minelli and Bortoletto 1988). Of the two families of euthycarcinoids, the Sottyxerxidae are more 'primitive' in possessing up to thirty-five post-cephalic somites. But being euthycarcinoids, they have attained six limb-free postabdominal segments. The trend for paedomorphic reduction in segment number is continued to the Euthycarcinoidea, with sixteen post-cephalic somites. The loss of segments from myriapods to euthycarcinoids accords with Demange's (1967, 1969) model of 'metameric reduction' in myriapods, in other words an evolutionary trend towards reduction of number of segments. Segment number does not change between the Euthycarcinoidea and the Hexapoda, just the number of appendages. The dorsal fusion of the cephalon, with six somites beneath one dorsal tergite (the head), is a further continuation of the trend to dorsal fusion apparent in the euthycarcinoid preabdomen. Boudreaux (1979) suggested that the tagmosis of the three gnathal segments could have occurred in a single step. In the sottyxerxids only diplosegments are known, but in the euthycarcinids, such as *Kalbarria*, triplosegments are developed. The gnathocephalon of the hexapods is equivalent to the triplosegments of euthycarcinoids, with dorsal fusion of three segments.

This overall reduction in variability of firstly, segment number and secondly, limb number between myriapods, euthycarcinoids and hexapods, combined with segment number and, in particular, appendage number becoming firmly fixed, parallels the phylogenetic 'hardening' of developmental regulation seen in another arthropod group, the Trilobita (McNamara 1986). Early trilobites, in particular Early Cambrian forms, show high variability in segment number within species, as well as between species. As forms evolved through the Cambrian, so the segment number became more fixed, firstly at the specific level, then at the supraspecific level. By the Ordovician, thoracic segment number largely had become fixed at the ordinal level. Such developmental 'hardening' (see McKinney and McNamara 1991) is likely to be a reflection of improved refinement in the control of developmental regulation.

Ecological and physiological factors

It might seem a little surprising, given the close morphological similarity between euthycarcinoids and hexapods, that more emphasis has not been given to the possible rôle of euthycarcinoids in hexapod evolution. One obvious reason is that prior to the discovery of *Kalbarria brimmellae*, the earliest fossil hexapod remains pre-dated the earliest euthycarcinoids. Whereas the earliest euthycarcinoids were thought to be Late Carboniferous, the earliest known hexapod is the Early Devonian collembolan *Rhyniella* from Scotland (Whalley and Jarzembowski 1981) and the earliest insect the wingless archaeognathan machilid from the Middle Devonian of New York State (Shear *et al.* 1984). (Some doubt exists over the validity of *Gaspea palaeoentognatha*, a specimen from the Early Devonian of Quebec that was described by Labandiera *et al.* 1988 as the first true insect, Jeram *et al.* 1990.) However, with the recognition of a euthycarcinoid in Silurian rocks that pre-date the earliest hexapod (Text-fig. 5), the case for euthycarcinoids being a link between early myriapods and the hexapods is strengthened.

Emerson and Schram (1990) and Schram and Emerson (1991) suggested that diplopodous uniramous, such as euthycarcinoids, may also have played a rôle in the evolution of arthropods that bear biramous appendages, perhaps having been close to a possible ancestor of the remipede crustacean *Tesmusocaris*. The fusion of the dorsal tergites in euthycarcinoids that resulted in a single dorsal segment being associated with a pair of ventral sternites could be seen as presaging the evolution of duplosegments in *Tesmusocaris* and thence biramous appendages in crustaceans as a whole.

While the case for the evolution of hexapods from euthycarcinoids can be made on anatomical and developmental grounds, there are ecological and physiological factors that need to be taken into consideration. The first potential problem lies with the fact that the earliest unequivocal myriapods from the Upper Silurian of Shropshire (Jeram *et al.* 1990) are interpreted, like the earliest hexapods,

as being terrestrial. Euthycarcinoids, on the other hand, have only been described from freshwater environments. The presence of the large flap-like setae on *Kottixerxes* argues for an active swimming way of life in this particular Carboniferous form. It would appear from this that on ecological grounds there are problems with suggesting that euthycarcinoids were ancestral to the hexapods. However, there are indications from the Tumblogooda Sandstone, in the form of fossil trackways, that suggest that Silurian euthycarcinoids were able to walk out of water.

There is strong evidence that eurypterid and other trackways from this unit were made subaerially (Trewin 1993). Trackways, similar in width to *Kalbarria brimmellae* and made by an animal with probably eleven walking appendages found close to the *K. brimmellae* specimen and at the same stratigraphical level, are most likely to have been made by a euthycarcinoid. The preservation and character of the trackways are like the eurypterid tracks, indicative of them having been formed subaerially. The relatively stout appendages of *K. brimmellae* are not inconsistent with their utilization for subaerial locomotion. The existence of aeolian sands overlaying fluvatile, track-covered sands and the preservation of very fine detail, argues for the trackways having been made in wet sand, but subaerially. It is quite possible that the preservation of *K. brimmellae* itself may have occurred by the animal having been overwhelmed in a sandstorm whilst traversing wet sand, resulting in rapid impression of the animal into the soft wet sediment, and immediate burial.

Another potential problem with the evolution of a group of initially terrestrial organisms from an aquatic group, is the question of respiration. It is not known how euthycarcinoids respired. However, as all other uniramians utilize tracheal respiration, it is possible that euthycarcinoids, like eurypterids (Selden 1985), may have possessed some form of pseudotracheal respiration in the aquatic environment, which preadapted them to terrestrial respiration. After all, forms that today are wholly terrestrial, such as the myriapods, had aquatic ancestors (Robison 1990). If the earliest hexapods were indeed very small then they probably, like other small arthropods, were able simply to respire directly through the thin cuticle.

The existence of true terrestrial arthropods, including centipedes and trigonotarbid arachnids in Late Silurian strata elsewhere (Jeram *et al.* 1990), combined with the probable amphibious behaviour of eurypterids and euthycarcinoids in Late Silurian strata in Western Australia, suggests that early attempts at colonization of land were perhaps more out of necessity to survive, than any attempt to colonize a vacant niche. Evidence is available (Trewin and McNamara work in progress) that eurypterids were walking in and out of pools of water on large sand flats. It is likely that as one pool dried up following river flooding, the eurypterids and other arthropods, including the euthycarcinoid, moved from pool to pool in an attempt to get back to the river.

The evidence that the early land arthropods were predominantly carnivorous (Jeram *et al.* 1990; Shear 1991), means that for early hexapods to survive in a generally hostile environment, it would have been necessary for them to adopt a cryptic habit to avoid predation pressure (Kukalová-Peck 1991). The likelihood that the early hexapods were very small, as the earliest fossils indicate (Whalley and Jarzembowski 1981, Shear *et al.* 1984), suggests that their evolution by paedomorphosis from euthycarcinoids may indeed have been by progenesis. Attainment of sexual maturity at an early growth stage would have meant not only retention of just three pairs of appendages, but also a very small body size. In fact it may have been this very small body size that was the prime target of selection, rather than the possession of three pairs of appendages. In an environment replete with predators, one of the most successful anti-predation strategies is the possession of a small body size. In what is likely to have been a very unstable environment, other *r*-selected life history strategies, such as rapid reproduction, combined with large numbers of offspring, would have been the ideal springboard for the rapid evolution of a major evolutionary novelty.

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KENNETH J. McNAMARA

Department of Earth and Planetary Sciences
Western Australian Museum, Francis Street
Perth, Western Australia 6000, Australia

NIGEL H. TREWIN

Department of Geology and Petroleum Geology
King's College
University of Aberdeen
Aberdeen AB9 2UE, UK

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NOTE ADDED IN PROOF

Schultka (1991) has described a further species of *Euthycarcinus* from the Upper Carboniferous of Nordrhein-Westfalen, Germany. He also favours a uniramian affinity for the Euthycarcinoidea, as a group separate from, but of equal taxonomic status to, the Myriapoda and the Hexapoda.

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